LIFE SCIENCES CONTRIBUTION 63

A. GORDON EDMUND

A Late Pleistocene Fauna from the Santa Elena Peninsula, Ecuador

ROYAL ONTARIO MUSEUM - UNIVERSITY OF TORONTO

ROM

Contribution No. 63
LIFE SCIENCES
ROYAL ONTARIO MUSEUM
UNIVERSITY OF TORONTO

A. GORDON EDMUND

A Late Pleistocene Fauna from the Santa Elena Peninsula, Ecuador

A. G. EDMUND is Associate Curator in charge of the Department of Vertebrate Palaeontology Royal Ontario Museum, University of Toronto.

PRICE *$1.00*

PRINTED AT THE UNIVERSITY OF TORONTO PRESS

Our knowledge of the Pleistocene fauna of the coastal regions of Ecuador is based largely on the material from the tierra brea found between Santa Elena and Salinas. This has yielded a great quantity of well-preserved bone which has been described by Spillmann (1931, 1948) and later by Hoffstetter (1952).

In 1958, the author was shown a new locality containing terrestrial vertebrates of Upper Pleistocene age in an apparently estuarine deposit, in association with marine fossils such as mollusks, echinoderm spines and shark teeth. With the cooperation of Mr. S. Marchant, Chief Geologist of the Anglo-Ecuadorian Oilfields Ltd., a small collection was made, sufficient to identify the fauna as being a late Pleistocene assemblage. The locality, shown in Fig. 1, is on the bank of a tributary of the dry Rio Engabao, about half way between the villages of Ancon and Atahualpa, approximately 80° 49′ W. longitude, 2° 18′ S. latitude.

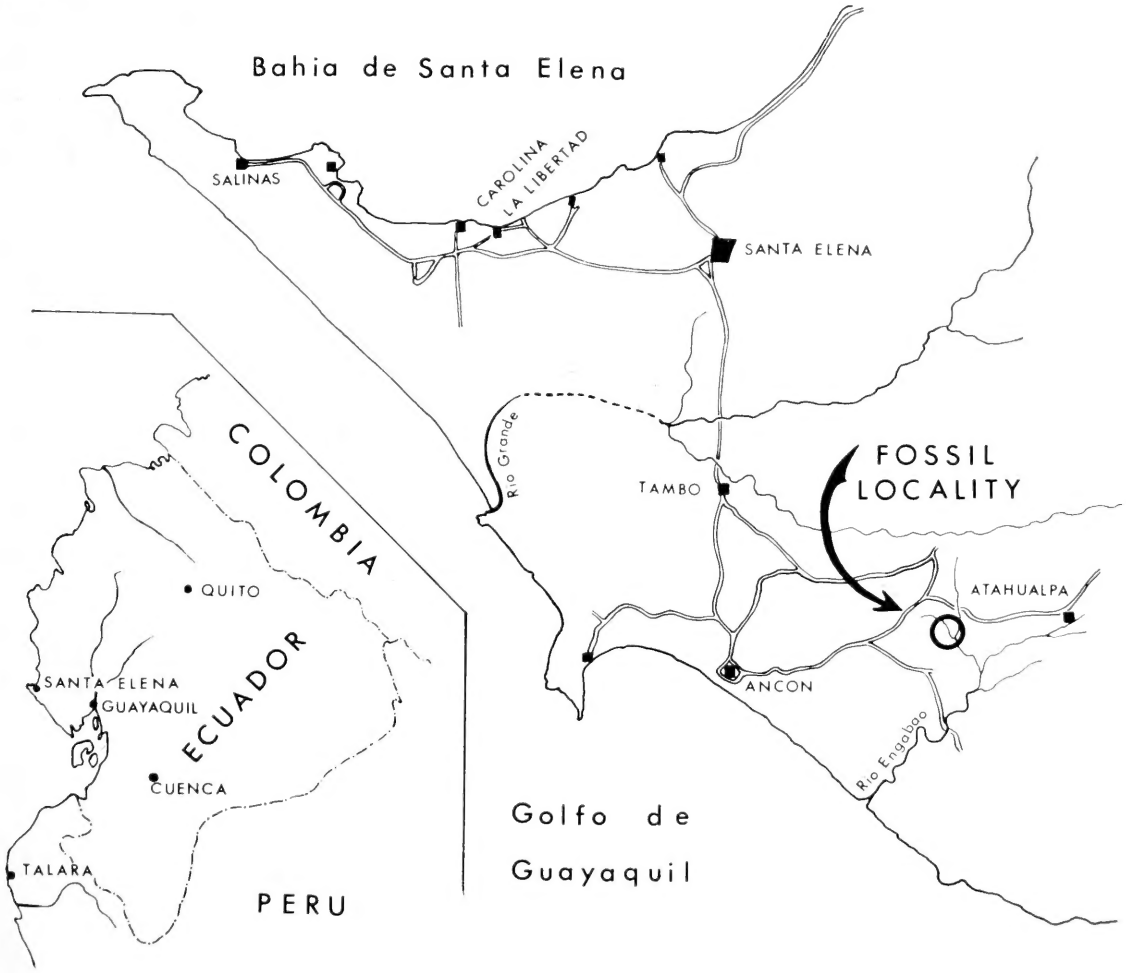

Figure 1. Map of the Santa Elena Peninsula, Ecuador.

The author returned to the same area in 1961. On this occasion, with the assistance of Mr. Neville Lindner, who succeeded Mr. Marchant, bones were found at three sites in the same tributary system, and a representative collection was secured. Since the localities are close together and of very similar lithology and horizontal level, they are considered to be contemporaneous. Some of the bones were incomplete *in situ*, and all were soft and fractured so that the larger elements had to be collected in plaster bandages. There was, however, little or no evidence of water wear, and the bones were remarkably undistorted.

Study of the bones was greatly facilitated by having for comparison two collections from the famous brea pits in the area between Salinas and Santa Elena. One, in the Escuela Politecnica Nacional (E.P.N.) in Quito, formed the basis of much of Hoffstetter's 1952 monograph. Thanks to the kindness of Prof. Gustavo Orcés, the author was able to measure and photograph a large part of this collection. The second reference collection is in the Royal Ontario Museum (R.O.M.) in Toronto, Canada, and was made in the vicinity of La Libertad (at or near Spillmann's "Coralito" locality) by the author in 1961. The geology of these vertebrate deposits has recently been studied by Dr. R. R. H. Lemon of the Royal Ontario Museum as part of a survey of the stratigraphic history of the Santa Elena Peninsula. Earlier studies were made by Spillmann (1948 *et al.*) and by Hoffstetter (1952), the latter giving a good bibliography of the subject.

The geology of the Santa Elena Peninsula is complex, and has given rise to conflicting opinions. The area is characterized superficially by numerous flat erosional surfaces, locally known as tablazos, found at different elevations. The correlation of these surfaces, some of which are faulted and raised to different levels, has been a source of dispute among the various geologists who have examined the area.

The Santa Elena Peninsula is underlain by a sequence of late Cretaceous and Early to Middle Tertiary sediments of various types including conglomerates, sandstones, greywackes and shales. These are complexly faulted so that the precise structure is still in some doubt despite the accumulation of much data from well logs. References to the subsurface work are summarized in Marchant (1961).

The Cretaceous and Tertiary rocks are overlain by several wave-cut terraces (tablazos) marking erosional surfaces developed at intervals during the Pleistocene when the land surface was considerably lower with reference to sea level than at the present time. The deposits associated with the marine terraces range from normal shelly beach sediments to fine-grained silts and poorly sorted sands of estuarine type. These merge landwards into downwash deposits, alluvial fans and fluvial gravels of Pleistocene to Recent age derived from the Cerros de Estancia.

The sediments containing the vertebrate remains described here are of estuarine type and were probably laid down by a large stream ancestral to the modern Rio Engabao, but with considerably greater run-off than the present stream. The vertebrate localities probably were near or at the mouth of the old river, and at or very close to sea level. Conditions very similar to those postulated for the Pleistocene Rio Engabao can be seen at the present time at Palmar, about eighteen miles to the north, where a small stream reaches the coast and spreads out into a brackish water swamp with mangroves.

The vertebrate remains found in the brea pits between Santa Elena and Salinas, although occurring in sands and silts soaked by pitch, were probably buried in a similar estuarine environment. In this case it is likely that a stream ancestral to the modern Rio Grande emerged in this general area and that there were estuarine swamps or salt flats at, or very close to, the sea level of that time. It seems probable that the introduction of the

petroleum into the deposit is a relatively recent phenomenon. The present elevation of the marine terrace at the brea pits (Spillmann's "Coralito" site) is approximately twenty-five feet above sea level, less than at the Rio Engabao vertebrate site. Thus it may be younger, but the precise ages of both localities await the results of radiocarbon determinations.

A detailed report on the Pleistocene geology of the Santa Elena Peninsula is being prepared by Dr. R. R. H. Lemon, who kindly supplied the geological notes summarized here. The author also wishes to acknowledge the very generous assistance of the management and staff of the Anglo-Ecuadorian Oilfields Ltd. In particular, I wish to thank Mr. S. Marchant and Mr. Neville Lindner, Chief Geologists, for providing information and making the innumerable arrangements which made possible the field work in the area. Dr. C. S. Churcher, Research Associate of the Royal Ontario Museum, provided information on the genera *Odocoileus* and *Smilodon* and supplied helpful criticisms of the manuscript. Thanks are also due to Professor Gustavo Orcés of the Escuela Politecnica Nacional in Quito for making that rich collection available for study. The turtle material was identified by Dr. Walter Auffenberg of the Florida State Museum, Gainesville, Florida.

CLASS MAMMALIA

Family MEGATHERIIDAE

Eremotherium cf. carolinense

The most abundant material from the Rio Engabao site is that of a large megathere. The definitions of the genera and species of megatheres are not on a firm basis, and are currently being studied by the writer. It is generally recognized, however, that the genus *Megatherium*, as typified by *M. americanum*, did not extend into the northern part of South America. The northern megatheres belong to a distinct genus, *Eremotherium*, known from Brazil, Venezuela, Colombia, and Ecuador, as well as Central America. Several species have been proposed, *E. carolinense* Spillmann and *E. rusconii* (Schaub) being the best known.

Hoffstetter (1952) described a smaller megathere from the coast of Ecuador under the name *Eremotherium elenense*. This has subsequently been collected in Peru by the writer, and appears to be very similar to other specimens from Chile and Bolivia. Because of its significantly smaller size, and other features, we can safely exclude this group from consideration here.

The material from Rio Engabao was compared with specimens of *Megatherium americanum* from Argentina, and with several populations of the genus *Eremotherium* from Ecuador, Colombia, Venezuela, Brazil and Panama. On the basis of the elements in the Rio Engabao fauna, it is possible to rule out the presence of *Megatherium*, and to assign the material to *Eremotherium*. Because of the great individual variation inherent in the megatheres, and because of the lack of more diagnostic elements in the Rio Engabao fauna, it is difficult to assign a specific name to the material. However, the tibia appears to indicate a much closer affinity to *E. carolinense* than to other species. Also, a well-preserved partial skull of *E. carolinense* in the Peabody Museum, Yale University (Y.P.M. 14159)

was collected in what appears to have been a similar type of deposit not very distant from the Rio Engabao site. Hoffstetter (1952) gives measurements of and illustrates a restored cast of this specimen (E.P.N., V.1508). For these reasons, the material from this site will be assigned to *E. carolinense*.

Many specimens of *Eremotherium* are now known from sites across the northern part of South America and through Central America into the south-eastern United States. These have often been given different specific, subgeneric and generic names, some of which will certainly prove to be synonymous. A review of the group is given in Hoffstetter (1952) but numerous other specimens have come to light since that date.

Material for comparison with the Rio Engabao megathere represents several populations. The well-known tar-seeps of coastal Ecuador, described by Hoffstetter (1952), lie near the town of La Libertad, between Salinas and Santa Elena, in the Santa Elena Peninsula. Collections from these seeps are in the Escuela Politecnica Nacional (E.P.N.) in Quito, Ecuador, and in the Royal Ontario Museum (R.O.M.) in Toronto, Canada. A Panamanian population is represented by the extensive collections from the Province of Herrera, Panama (Gazin, 1956) deposited in the Museo Nacional de Panama (M.N.P.) and the United States National Museum (U.S.N.M.) and has been assigned to *E. rusconii* (Schaub). The Venezuelan material does not represent a distinct population, but rather scattered occurrences which seem to represent the same species at about the same geological age. These occurrences include the type of *Eremotherium rusconii*, the material from San Miguel in the museum of the Collegio de La Salle in Barquisimeto, both from the Estado de Lara, and the Muaco fauna (Estado de Falcon) collected by Royo y Gomez and Cruxent and now in the Universidad Central, Caracas. The Colombian material is best represented by an articulated skeleton in the Museo de Servicio Nacional de Geologia, Bogota (M.G.N. 2000), excavated by Stirton and Royo y Gomez in Huila province, and referred to *E. rusconii* (de Porta, 1961). The Brazilian specimens have been referred to various species (*rusconii, laurillardi, lundi*, etc.) but all may prove to be *rusconii*. As with the Venezuelan specimens, the Brazilian material is from numerous localities of uncertain geological ages. Most of it is in the Museu Nacional in Rio de Janeiro (M.N.R.J.).

Material assigned to *Eremotherium carolinense* includes the following:

An Isolated Tooth, R.O.M. 3895, of the usual rectilinear pattern with two sharp transverse ridges. Comparison with cranial material from the Santa Elena Peninsula confirmed it as a typical second upper tooth. The size agrees well with that of similar teeth from Venezuela, Colombia and Panama. Antero-posterior length is 43.4 mm., width at anterior ridge is 49.1 mm., and width at posterior ridge is 49.2 mm.

A First Cervical Vertebra (atlas), R.O.M. 3896, recovered in fragmentary condition, lacking both wings. There is little difference in the form and measurements of this bone between any of the known large megatheres. The essential measurements fall into the ranges of the populations from the Santa Elena Peninsula and from Panama. Fifteen measurements were compared, five of the more important being shown in Table I. The Rio

TABLE I. Comparative measurements of the first cervical vertebra (atlas)

	Eremotherium rusconii from Panama				*Eremotherium carolinense* from Santa Elena Peninsula, Ecuador				R.O.M. 3896 Rio Engabao specimen
	Max.	Min.	N	$\bar{X}$	Max.	Min.	N	$\bar{X}$	
Width across Prezygapophyses	185	160	3	175	179	143	5	159	154
Greatest height	139	115	3	126	141	115	5	126	115
Length of Prezygapophyses	104	85	2	94	95	80	5	86	86
Width of Prezygapophyses	56	40	3	50	65	54	5	58	47
Width across Postzygapophyses	213	168	3	185	192	179	5	184	184

Engabao atlas appears to belong to a mature individual, but since it lacks the wings one cannot determine the degree of fusion of the epiphyses.

The Sixth Cervical Vertebra, R.O.M. 4304, is almost completely preserved. The morphology and dimensions are almost exactly the same as those of R.O.M. 4311, a specimen of *E. carolinense* from the brea pits near La Libertad, Ecuador. Table II gives the essential measurements.

TABLE II. Measurements of the sixth cervical vertebra of *Eremotherium*

	Rio Engabao Specimen R.O.M. 4304	*Eremotherium carolinense* R.O.M. 4311, Santa Elena Peninsula
Greatest height	190	204
Width across transverse processes	231	—
Height of centrum	72	*68
Length of centrum	73	*72
Greatest width of neural canal	73	75
Width across postzygapophyses	138	147

*Estimated measurement.

Other axial material definitely referrable to *Eremotherium* includes the following:

4307 Cervical vertebra III, centrum
4309 Mid-thoracic vertebra, centrum
4308 Caudal vertebra, about No. 12, centrum
4306 Proximal caudal vertebra with part of the neural arch
3899 Sternal element; agrees in size and form with *Eremotherium* specimens from the Ecuadorian brea pits.

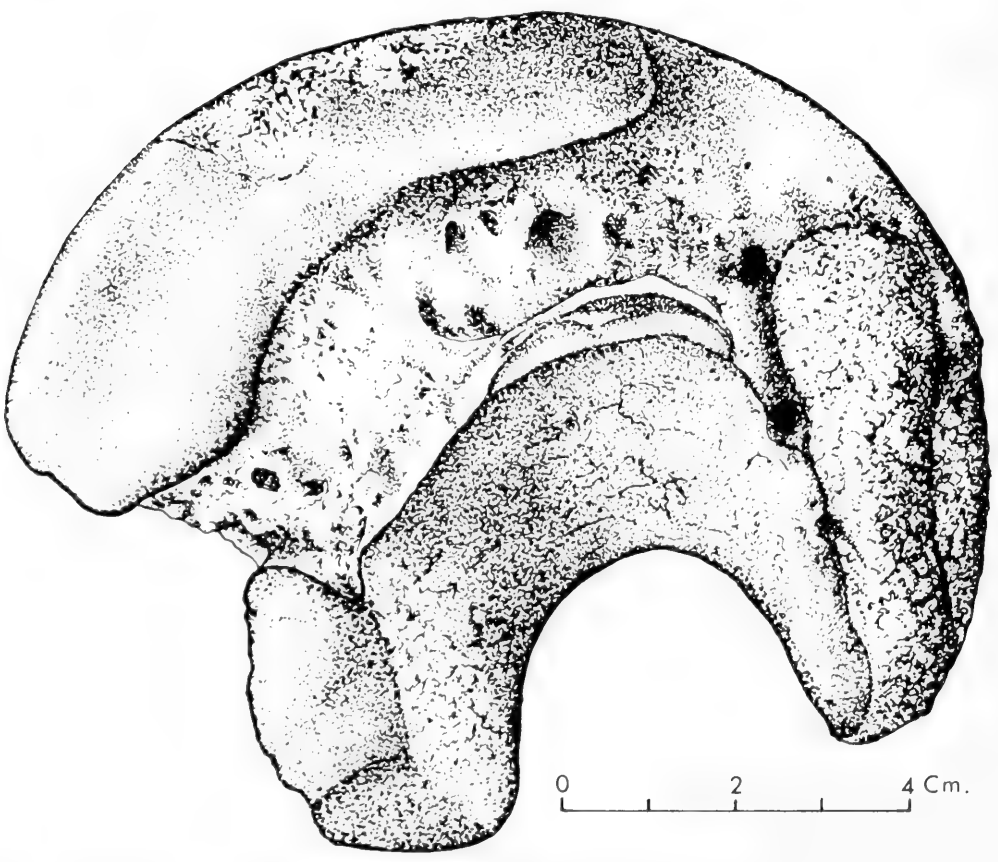

Figure 2. Medial view, right lunar of *Eremotherium*, R.O.M. 3898.

TABLE III. Comparative measurements of lunar bones

	Eremotherium rusconii from Panama				*Eremotherium carolinense* from Santa Elena Peninsula, Ecuador				*Eremotherium rusconii* M.G.N. 2000, Colombia	R.O.M. Rio Engabao specimen
	Max.	Min.	N	$\bar{X}$	Max.	Min.	N	$\bar{X}$		
Length of radial articulation	130	120	7	127	149	123	4	138	121	119
Width of radial articulation	89	79	7	85	97	74	4	90	90	88
Length of scaphoid articulation	101	85	7	95	115	85	4	108	91	81
Width of scaphoid articulation	30	27	7	29	35	30	4	31	31	26
Height of magnum articulation	84	77	7	80	85	72	4	80	79	68
Width of magnum articulation	51	41	7	49	51	44	4	47	35	44
Height of unciform articulation	83	73	7	80	83	67	4	72	79	67
Height of cuneiform articulation	63	53	7	58	63	53	3	58	—	55
Width of cuneiform articulation	45	28	7	36	43	30	4	37	—	30

4310 Occipital condyle, damaged, 93 mm. long.

THE ANTERIOR LIMB is represented by a right lunar, fourth metacarpal, and phalanx 2, digit IV.

The Lunar, R.O.M. 3898, is perfectly preserved and closely resembles the specimens of *Eremotherium* from Colombia, Panama and Ecuador. As shown in Fig. 2, the main contact with the scaphoid is distinctly separated from the distal articulations by a broad and rather deep groove, the floor of which contains several deeply penetrating canals. There are two secondary articulations with the scaphoid, a larger dorsal facet, 21 × 28 mm. and a narrow ventral one about 6 × 25 mm. Both are continuous with the facet for the magnum, but are clearly defined from it. These secondary articulations are common in all megatheres, and are quite variable in size and configuration.

The articulations of the lunar are identical in all Pleistocene megatheres, with only minor proportional differences. Measurements of comparable material are shown in Table III. These indicate that the lunar from the Rio Engabao site is from a rather small individual, but that it belongs with the populations of *Eremotherium* from Colombia, Ecuador, and Panama.

Metacarpal IV, R.O.M. 3171 (Fig. 3) is perfectly preserved, except for some damage to the proximal articulations. Unlike the lunar, the fourth

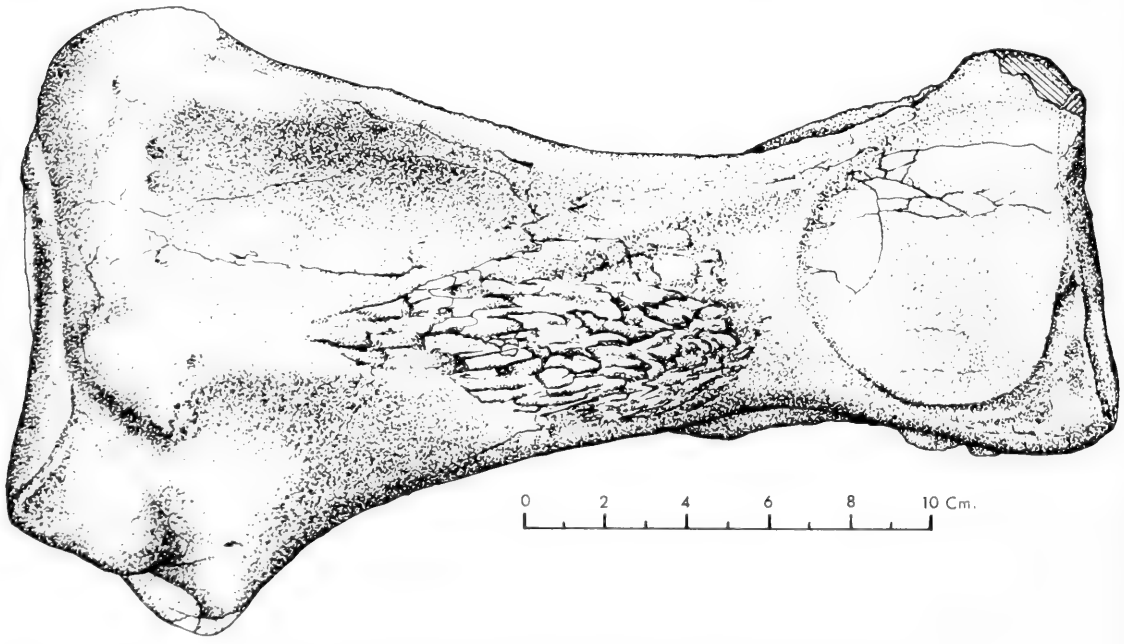

Figure 3. Lateral view, left metacarpal IV of *Eremotherium*, R.O.M. 3171.

metacarpal of *Eremotherium* is distinguishable from that of *Megatherium*. The general form, length, and relationships of the articulations are the same in both genera. Measurements of the bone from the Rio Engabao site were compared with those of several specimens of *M. americanum*. In the latter, the bone is generally of lighter construction, and the articulations, especially those for the third metacarpal and unciform, are smaller.

The Rio Engabao metacarpal was compared with those from other populations of *Eremotherium* (Table IV), and the proportions were found to be in excellent agreement. The Rio Engabao bone obviously belongs to a large individual, but it is not beyond the range expected for this highly

TABLE IV. Comparative measurements and proportions of metacarpal IV

	Eremotherium rusconii from Panama				*Eremotherium carolinense* from Santa Elena Peninsula, Ecuador				Type of *Eremotherium rusconii* (Cast)	*E. rusconii* M.G.N. 2000 Colombia	R.O.M. 3171 Rio Engabao specimen
	Max.	Min.	N	$\bar{X}$	Max.	Min.	N	$\bar{X}$			
Greatest length	320	252	7	287	283	263	4	272	295	248	286
Proximal height*	39	30	7	34	38	33	4	35	34	38	36
Proximal width*	34	30	7	32	36	29	4	33	—	36	31
Distal height*	55	47	6	50	55	51	4	52	48	55	55
Dorso-ventral height of unciform facet*	32	26	5	29	30	25	4	27	31	27	30
Dorso-ventral height of Metacarpal V facet*	30	23	6	27	24	21	4	22	—	21	24
Ratio, Metacarpal IV facet $\frac{\text{Height}}{\text{Width}}$	1.4	1.1	5	1.2	1.3	1.2	4	1.3	1.4	1.2	1.4
Ratio $\frac{\text{Proximal height}}{\text{Proximal width}}$	1.15	0.99	5	1.06	1.17	1.00	4	1.06	—	.96	1.14

*Expressed as % of greatest length.

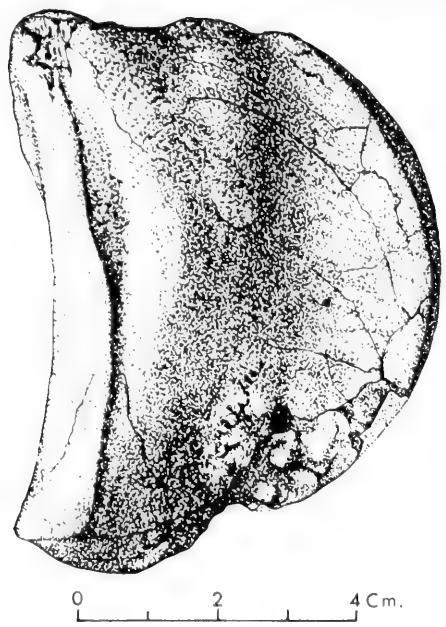

Figure 4. Lateral view, right phalanx 2, digit IV of *Eremotherium*, R.O.M. 3170.

variable group. It seems impossible however, to distinguish between the various populations of *Eremotherium* from the measurements in Table IV.

Phalanx 2, Digit IV, R.O.M. 3170, is illustrated in Fig. 4. It is assigned to *Eremotherium* on the basis of its general form, and on the measurements in Table V. As with the corresponding metacarpal, it represents a large individual, but not one too large to be part of either of the populations for which comparative measurements are available. Morphologically it is indistinguishable from them.

TABLE V. Comparative measurements of phalanx 2, digit IV, manus, of *Eremotherium*

	E. rusconii, Panama Mean of 2 specimens	*E. carolinense*, *Santa Elena* Peninsula, Ecuador Mean of 4 specimens	R.O.M. 3170 Rio Engabao specimen
Proximal height	80	74	83
Proximal width	75	67	75
Length	52	51	55
Proximal articular width	65	62	63
Proximal articular height	72	68	77
Distal articular width	62	55	68
Distal articular height, lateral	58	63	69
Distal articular height, medial	50	49	62

The corresponding phalanx in *Megatherium americanum* (based on a single specimen in Museo de La Plata, MLP 2-190) is of about the same length, (52 mm.) but is about twenty percent smaller in most other dimensions. This, too, agrees with the lighter construction of the fourth metacarpal in *Megatherium*.

THE POSTERIOR LIMB is represented by a right tibia, fibula and a fifth metatarsal.

The fused tibia and fibula, R.O.M. 4312, is well-preserved, but lacks most of the fibula (Fig. 5). The bone is from a mature individual, as shown by the well-closed epiphyseal sutures. However, it is not especially

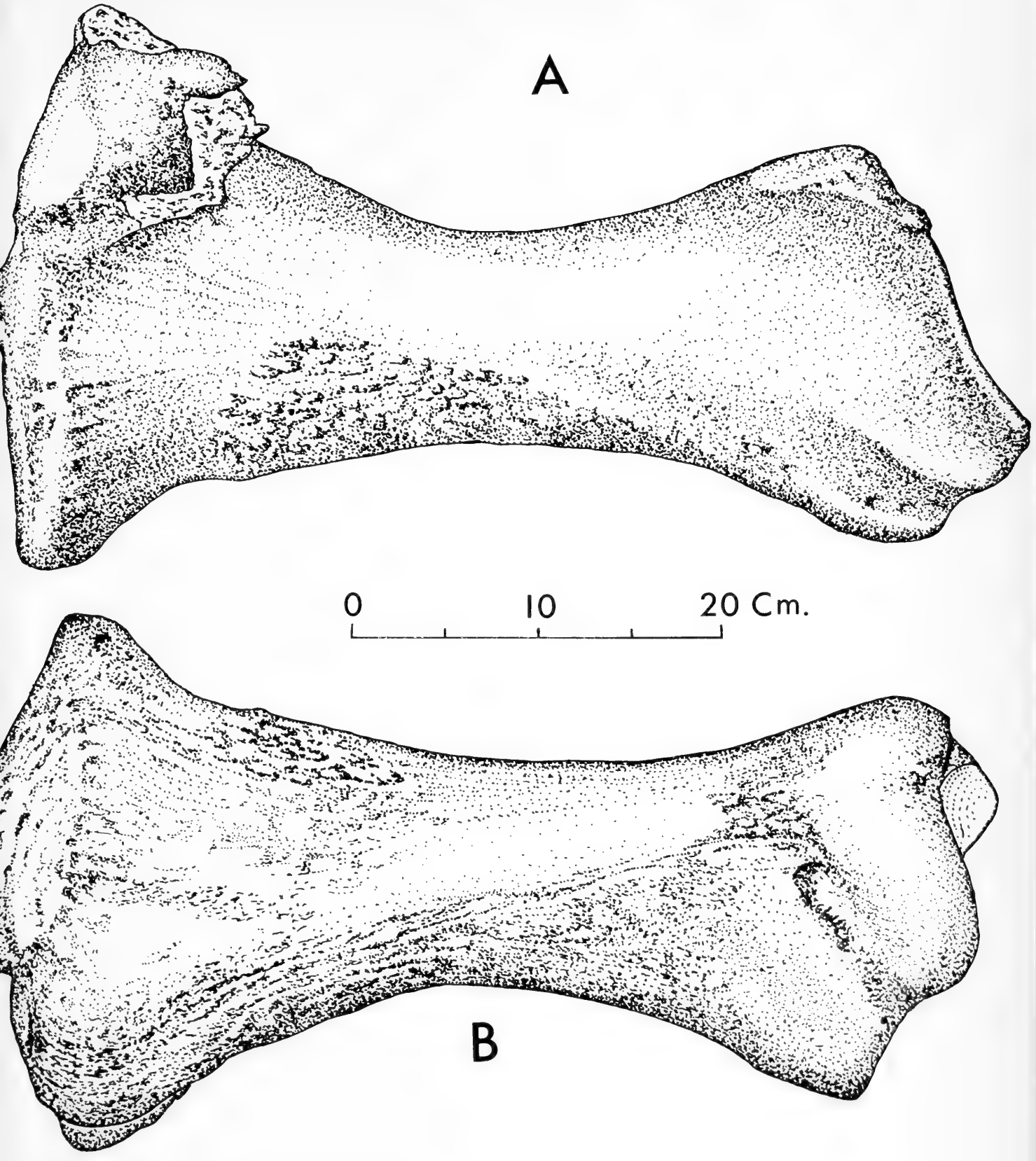

Figure 5. Tibia of *Eremotherium*, R.O.M. 4312. A—anterior view. B—posterior view.

TABLE VI. Measurements of tibiae expressed as percentages of total length

	Eremotherium rusconii from Panama				*Eremotherium carolinense* from Santa Elena Peninsula, Ecuador				*E. rusconii* M.G.N. 2000 Colombia	R.O.M. 4312 Rio Engabao specimen
	Max.	Min.	N	$\bar{X}$	Max.	Min.	N	$\bar{X}$		
Total length (100%) in mm.	624	512	6	573	598	580	4	591	530	561
Proximal width	64	58	6	62	60	56	3	58	—	58
Proximal articular width	53	48	5	51	49	43	4	47	51	47
Antero-posterior length medial femoral facet	29	27	4	28	29	24	4	27	28	26
Transverse width medial femoral facet	24	21	5	23	21	20	4	21	22	21
Distal articular width	34	30	5	32	32	29	4	30	33	—
Antero-posterior length of large trochlear facet	37	30	6	34	35	32	4	33	35	34

rugose, and therefore not of particularly advanced age. The morphology of the tibia is quite constant in all of the large megatheres studied, and no obvious differences were noted between those of *Megatherium* and *Eremotherium*. The description of Owen (1859, p. 813) applies equally well to both. Measurements of the tibiae of *Megatherium americanum* agreed fairly closely with those of the several specimens of *Eremotherium*, except that the proximal width and proximal articular width are both significantly greater in the former. The proportional measurements given in Table VI show closest agreement between the Rio Engabao specimen and the fauna from the Ecuadorian brea pits. The proportional measurements for the proximal width, proximal articular width, and length of the median femoral facet all fall well within the range of the specimens of *E. carolinense*, but are completely or almost completely out of the range for the Panamanian material. This is one of the few instances where there appears to be a valid distinction between these faunas, as based on elements in the Rio Engabao fauna. Thus, the tibia may be assigned to an individual from the same population as the specimens of *E. carolinense* from the brea pits of the Santa Elena area.

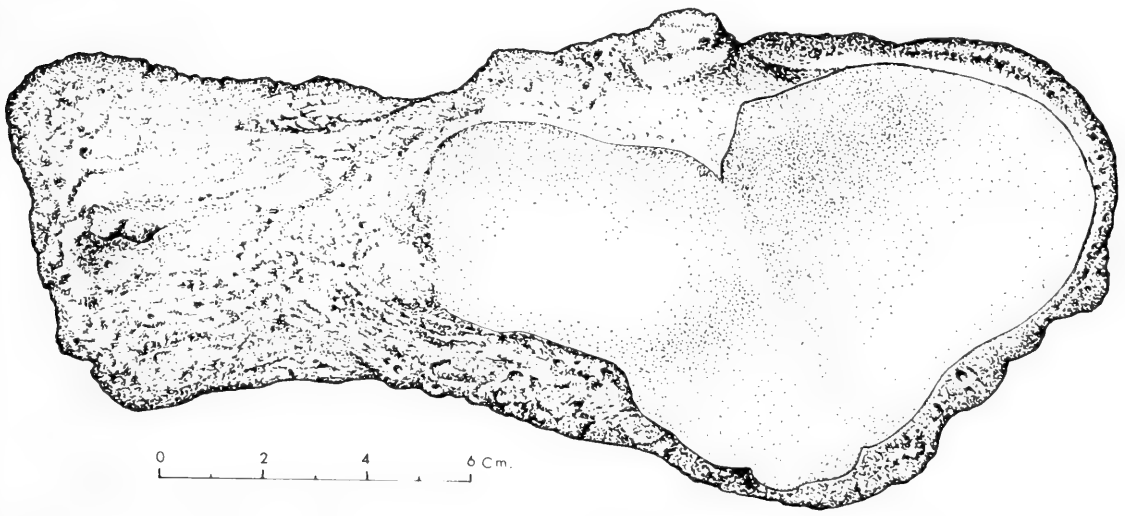

Figure 6. Medial view, right metatarsal V of *Eremotherium*, R.O.M. 3892.

The Fifth Metatarsal is perfectly preserved, and represents a thoroughly mature individual, as shown in Fig. 6. The Rio Engabao metatarsal was compared in detail with seventeen others representing *Eremotherium* populations from Panama, Colombia, and the Santa Elena Peninsula, Ecuador, as well as *Megatherium americanum* from Argentina. The measurements and proportions of all of these were remarkably similar, and no valid distinction between populations could be detected on the basis of elementary statistics. The measurements of the Rio Engabao specimen are given in Table VII.

The Rio Engabao megathere material can confidently be assigned to the genus *Eremotherium* on the basis of several elements. Reference to the species *E. carolinense* is likely on the basis of measurements of the tibia, and on the geographic proximity of the site to that of the type material.

TABLE VII. Measurements of metatarsal V, *Eremotherium* sp. R.O.M. 3892

Length	221
Proximal height	93
Distal height	70
Distal width	69
Length of cuboid articulation	71
Height of cuboid articulation	68
Length of Metatarsal IV articulation	59
Height of Metatarsal IV articulation	65
Height of distal articulation	27
Width of distal articulation	20

Family DASYPODIDAE

Pampatherium cf. occidentale

This species is represented by a single scute (R.O.M. 3891) from one of the fixed shields. I have assigned it to Hoffstetter's species purely on geographical grounds, since it is impossible to be more precise on the basis of an isolated scute.

The specimen measures 45 mm. long, 39 mm. wide, and 10.8 mm. in maximum thickness. It is apparently from close to the margin of the shield, since the central raised portion is displaced well toward one end. The surface pattern is typical of the genus, agreeing in detail with the numerous scutes from the brea pits of Talara, Peru and the Santa Elena Peninsula of Ecuador, as well as with those from North America.

The generic name *Pampatherium* Ameghino 1875 has been adopted in preference to *Chlamytherium* Lund 1839 or *Holmesina* Simpson 1930. *Chlamytherium*, which appears to have been a misprint for *Chlamydotherium*, was used in 1838 by Bronn for a glyptodont, and thus becomes a *nomen nudum*. As pointed out by Paula Couto (1954) the valid name is *Pampatherium* Ameghino 1875.

Holmesina was proposed by Simpson 1930 for the chlamytheres of North America. The great similarity between the North American and Ecuadorian forms was recognized by Hoffstetter (1953), and the Ecuadorian species *C. occidentale* transferred to *Holmesina*. The writer has recently examined most of the available specimens, and found little evidence to support the generic difference between classical *Chlamytherium* and the species referred to *Holmesina*. Until a more comprehensive study has been made of new material now on hand, the genus *Pampatherium* is used for the Ecuadorian material, and the Rio Engabao scute is assigned to the species *occidentale* on the basis of size, form and geographical location.

Family EQUIDAE

Equus (Amerhippus) cf. santae-elenae

Two specimens were recovered, a single tooth, R.O.M. 3169, and part of a proximal phalanx, R.O.M. 3894.

The tooth is a badly worn lower third molar, shown in Fig. 7. It resembles Hoffstetter's species *Equus (Amerhippus) santae-elenae*, but there are minor differences. The measurements are given in Table VIII.

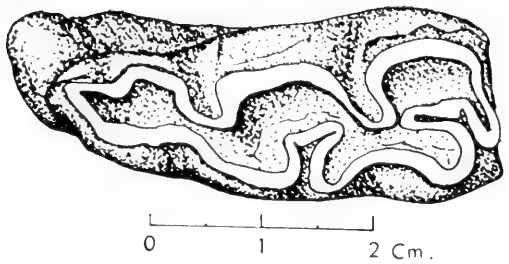

Figure 7. Lower third molar, *Equus* (*Amerhippus*) *santae elenae*, R.O.M. 3169.

TABLE VIII. Measurements of *Equius* molar from Rio Engabao compared with specimens of *E.* (*A.*) *Santae-elenae*

	E. (*A.*) *santae-elenae*				Rio Engabao Specimen R.O.M. 3169
	Usual range*		Two very old specimens*	R.O.M. 3490F Talara, Peru	
	Max.	Min.			
Antero Posterior-length	31.3	29.6	32.6–35.5	36.0	36.1
Width	15.8	13.4	16.0	15.5	16.0

*From Hoffstetter 1952.

No other species of horse was found to resemble the Rio Engabao specimen. The geographically closest species, *E. andium* is considerably smaller and not morphologically similar. Also, it frequented higher altitudes, and thus is unlikely to be found in a coastal fauna. The measurements of R.O.M. 3169 indicate reasonably good agreement with specimens of *E.* (*A.*) *santae-elenae* from both Peru and Ecuador.

The cusp pattern, however, is unusual in one detail. The entoconid (Hoffstetter's terminology) is less well developed in the Rio Engabao specimen than in either the specimens illustrated by Hoffstetter (1952) or those from Talara, Peru. In both of these latter groups of specimens the enamel of the entoconid is folded inward and posteriorly for about 3 millimetres. This fold is completely lacking in R.O.M. 3169. Possibly this is a feature of advanced age, since the crown is very badly worn. The most nearly comparable tooth from Talara, Peru, and identified as *E.* (*A.*) *santae-elenae*, has at least an additional one centimetre of its crown height remaining. However, Hoffstetter illustrates the lower dentition of a 15 year old individual of the same species with a well marked fold on the entoconid. The crown height of this tooth is unknown.

Specimen R.O.M. 3894 is a fragment of the distal end of a proximal phalanx of the right manus. It agrees well with specimens of *E.* (*A.*) *santae-elenae* from Talara, Peru. Unfortunately, however, it is of no value in determining the specific identity of the animal.

The horse specimens from Rio Engabao can be confidently assigned to *Equus* (*Amerhippus*), and at least tentatively to the species *santae-elenae*.

Family CERVIDAE

Odocoileus cf. salinae

Two specimens, a right astragalus and an antler tine, indicate the presence of a deer similar to that found in the brea pits of Peru and Ecuador. Since no more diagnostic material was recovered, it is impossible to assign con-

fidently a specific name to the Rio Engabao cervid. However, the astragalus was compared with the figures of Frick (1937), Hoffstetter (1952) and with the original material from Peru described by Churcher (1962) and it agrees well in all respects with *Odocoileus salinae* Frick.

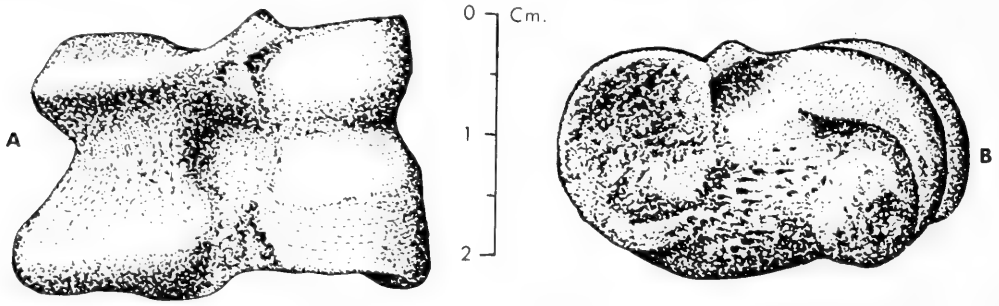

Figure 8. Right Astragalus of *Odocoileus* cf. *salinae*, R.O.M. 3168. A—dorsal view. B—medial view.

TABLE IX. Measurements of the *Odocoileus* astragalus from Rio Engabao compared with those from Talara, Peru and the Santa Elena Peninsula

	Talara, Peru Churcher (1962)				Santa Elena Peninsula Hoffstetter (1952)				Rio Engabao R.O.M. 3168
	Min.	Max.	N	$\bar{X}$	Min.	Max.	N	$\bar{X}$	
Proximo-distal length	31.2	34.5	10	33.2	30.7	35.8	3	—	34.4
Distal width	20.0	22.9	10	21.0	18.8	23.2	3	—	22.3

The astragalus, R.O.M. 3168, shown in Fig. 8, is from a mature individual and well preserved. The measurements given in Table IX show that it lies well within the range of *O. salinae*. Churcher points out that Hoffstetter's material from the brea pits of the Santa Elena Peninsula represents larger individuals than that from Peru. The Rio Engabao astragalus is at the upper end of the range of measurements for the Peruvian material, but is well within the range of that from Ecuador. Although it is based on very slight evidence, one might conclude that the Rio Engabao specimen belongs to the population of slightly larger individuals characteristic of the Santa Elena region of Ecuador.

The antler fragment, R.O.M. 3892, is part of the tip of the main, or terminal tine, 54 mm. long. At the proximal end it is somewhat triangular in section and measures about 11.6 mm. in greatest thickness. This is about one-third larger than a comparable fragment from Peru, but this measurement is extremely variable with sex and age.

Family MUSTELIDAE

cf. Lutra sp.

A small carnivore is represented by an isolated vertebral centrum (R.O.M. 3172), lacking all of the neural arch, spines, etc. It measures 21.4 mm. long, and about 15 mm. across the central faces. On comparison with modern material it proved to be quite similar to the eleventh thoracic vertebra of *Lutra*, both in size and form. If it is assignable to this genus it represents a large form, but no larger than some present-day species in South America. The fragment, however, is insufficient to do more than indicate the probable occurrence of an otter in the Rio Engabao fauna.

Family FELIDAE

Smilodon neogaeus (Lund)

The sole evidence for this species is a perfect specimen of the proximal phalanx of digit 1, R.O.M. 3890. However, this bone (Fig. 9) is quite distinctive and agrees with the large series from Talara, Peru. The measurements given in Table X, fall well within the range for *S. neogaeus*. The measurements for the Talara material are supplied by Dr. C. S. Churcher, whose revision of the genus *Smilodon* is nearing completion.

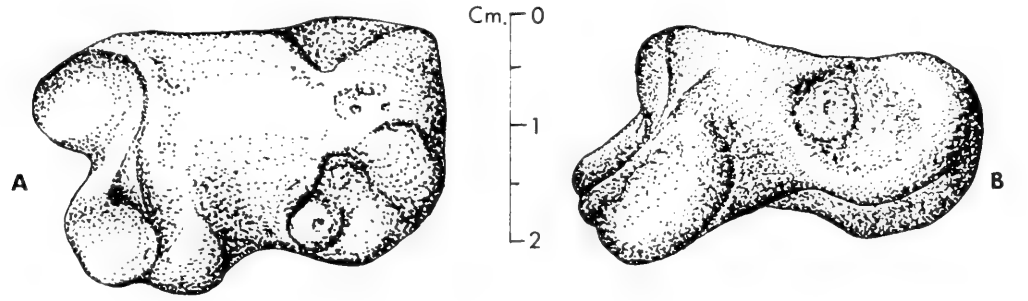

Figure 9. Proximal phalanx, digit 1 of manus of *Smilodon neogaeus*, R.O.M. 3890. A—dorsal view. B—medial view.

TABLE X. Measurements of the proximal phalanx, digit I, manus of *Smilodon*

	Specimens from Talara, Peru			R.O.M. 3890 Rio Engabao
	Maximum	Minimum	$\bar{X}$*	
Total length	39.6	34.7	37.3	36.5
Proximal width	27.4	23.2	24.8	24.1
Proximal height	21.9	18.9	20.2	19.0
Distal width	26.0	21.8	23.4	22.5
Distal height	17.2	14.1	15.7	14.3

*N = 25.

Panthera atrox was also present in North-Western South America, as revealed by a fine skull and other elements collected by the writer at Talara, Peru, in 1958. The proximal phalanx of this animal is compared with that of *Smilodon* in Merriam & Stock (1932), and there is no doubt that they are morphologically distinguishable. The Rio Engabao specimen clearly does not belong to *Panthera atrox*.

Hoffstetter (1952), had very little *Smilodon* material and did not attempt to assign a specific name to the material from the Ecuadorian brea pits. The writer was, however, fortunate in recovering material of excellent diagnostic value from that site in 1961, and there is no question that it also belongs to *S. neogaeus*.

CLASS REPTILIA

The only reptiles in the fauna are chelonians, represented by fragments of shells and a few limb bones. These have been examined by Dr. Walter Auffenberg. One tortoise is present, tentatively assigned to *Geochelone* (*Testudo*) cf. *G.* (*T*) *gallardoi* on the basis of parts of the plastron and carapace. Also present is *Geoemyda* sp., as well as some unidentifiable turtle scraps.

CONCLUSIONS

The list of terrestrial fauna is as follows:

Class Mammalia

Order Carnivora

Smilodon neogaeus

cf. *Lutra* sp.

Order Perissodactyla

Equus (*Amerhippus*) *cf. santae-elenae*

Order Artiodactyla

Odocoileus cf. salinae

Order Edentata

Eremotherium cf. carolinense

Pampatherium cf. occidentale

Class Reptilia

Order Chelonia

Geochelone cf. gallardoi

Geoemyda sp.

Turtle indet.

The scattered and ill-sorted nature of the vertebrate remains, with an admixture of marine material, argues strongly for the estuarine environment of the deposit. Probably there was a wide muddy delta with numerous small islands and shallow water-courses at or near sea level.

The comparatively rich vegetation of such an area no doubt attracted a wide variety of herbivores with their attendant carnivores. On the death of these animals, the skeletons probably were shifted about as they fell apart, and were rapidly buried in the mud.

The fauna is a selection of common late Pleistocene vertebrates, and is especially similar to that from the better-known brea pits near La Libertad. No recognizable specimens of *Mastodon* or *Scelidodon* were found, but since the number of specimens recovered was relatively small, they could have been excluded from the sample on the basis of chance alone. The fauna is quite distinctively a coastal one, with none of the highland mastodons or horses, or *Glossotherium* (*Oreomylodon*) *wegneri*.

The age of the fauna cannot be determined with any certainty, but it is obviously fairly late, since there are no remains of *Macrauchenia*, toxodonts or other animals which persisted until fairly late in the Pleistocene elsewhere. On the other hand there are remains of *Smilodon* and *Odocoileus*, both relatively recent immigrants, thus indicating a late Pleistocene age.

Many faunal collections of Pleistocene age are now known from the northern part of South America, but these have received scant attention. Only a few have been published, and little attempt has been made to correlate them. It is hoped that a series of papers, similar to the present publication, will permit description of the fauna and stratigraphy of these occurrences with a view to understanding better the palaeozoogeography of this interesting area.

REFERENCES

CHURCHER, C. S., 1962
Odocoileus salinae and *Mazama* sp. from the Talara tar seeps, Peru. Royal Ontario Mus., Life Sci. Div., Contrib. 57, 1–27.

FRICK, C., 1937
Horned Ruminants of North America. Bull. Amer. Mus. Nat. Hist. 69: 205–214.

HOFFSTETTER, R., 1952
Les Mammifères Pléistocènes de la République de l'Équateur. Soc. Géol. France. Mém. 66: 1–391, 8 pls.

——— 1953
Sur la présence d'un Tatou géant du genre *Holmesina* dans le Pléistocène de l'Équateur (Amérique du Sud). Soc. Géol. France. C.R. Somm. 6: 101–2.

MARCHANT, S., 1961
A photogeological analysis of the structure of the western Guayas Province, Ecuador: with discussion of the stratigraphy and Tablazo formation, derived from surface mapping. Quart. J. Geol. Soc. London 466; 215–232.

MERRIAM, J. C. AND STOCK, C., 1932
The Felidae of Rancho La Brea. Carnegie Inst. Wash., Publ. 422: 1–231, 42 pls.

PAULA COUTO, CARLOS DE, 1954
Megaterios Intertropicais do Pleistoceno. Anais da Academia Brasileira de Ciencias 26, 3: 447–463.

SIMPSON, G. G., 1930
Holmesina septentrionalis, extinct giant armadillo of Florida. Am. Mus. Novit. 442: 1–10.

SPILLMANN, F., 1931
Die Säugetiere Ecuadors im Wandel der Zeit. t.I: 1–112. Quito, Univ. Central.

——— 1948
Beiträge zur Kenntnis einer neuen gravigraden Reisensteppentieres (*Eremotherium carolinense* gen. et. sp. nov.), seines lebensraumes und seiner lebensweise. Paleobiologica, 8: 231–279.